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Ticks or lions: trading between allogrooming and vigilance in maternal care

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Behavioural adjustments to predation risk may impose costs on prey species. While the vigilance–foraging conflict has been extensively investigated, other important fitness-related behaviours exclusive to scanning, such as grooming, have been overlooked. Yet, risk perception is expected to be more accurately assessed in these contexts as food-related parameters should not interfere. We studied individually recognizable impalas, *Aepyceros melampus*, and questioned the factors that shape maternal decision making in two exclusive components of maternal care with high benefits and costs: scanning for predators and grooming offspring to remove parasites. While studies generally infer prey alertness level, used as a proxy of risk perception, from the observed investment in vigilance, the vigilance–allogrooming context gave us the opportunity to directly assess alertness during the time spent head-up, and then to investigate its sources of variation and its consequences for allogrooming probability. We found a strong decrease in allogrooming probability when maternal alertness increased. Mothers were more alert in open (grassland) than in closed (bushland) habitats at a large scale. Increasing group size led both to lower maternal alertness and higher proportion of suckling time spent allogrooming, but only when surrounded by low vegetation, the reverse being true in high vegetation. Finally, mothers suckling female calves were more alert. Our results underline the determinant role of habitat, shaping both offspring predation risk and the relative conspicuousness or protective value of group mates. We discuss the potential fitness costs associated with the antipredator–antiparasite trade-off faced during maternal care. Our results suggest that prey behaviours other than foraging are essential to identify factors shaping risk perception.

Several recent studies have pointed out that the costs of antipredator behaviours developed by prey species could be at least as important as direct killing by predators in shaping their population dynamics (e.g. Creel & Christianson, 2008). Behavioural adjustments to predation risk encompass many aspects, from habitat selection to vigilance behaviour. Habitat selection may impact prey fitness when individuals trade food quality/quantity for safety (e.g. Hamel & Côté, 2007). Antipredator vigilance behaviour is expected to reduce the amount of time available for other time-consuming activities, including important fitness-related behaviours. For instance, vigilance and foraging are classically expected to conflict because foraging requires visual attention and involves a head posture that generally shortens visual field. The magnitude of the costs to food intake rate associated with vigilance behaviour and the factors shaping the decision to engage in vigilance while foraging have been extensively investigated in the past few decades (Beauchamp, 2015), as these decisive behaviours are relatively easy to observe in many free-ranging animals.

Yet, vigilance behaviour conflicts with other fitness-related behaviours such as grooming. The removal of ectoparasites is one of the main functions of grooming (e.g. Mooring, McKenzie, & Hart, 1996). Ticks may strongly impact host fitness (e.g. Norval, Sutherst, Kurki, Gibson, & Kerr, 1988; Norval, Sutherst, Kurki, Kerr, & Gibson, 1997) through blood removal and disease transmission (Hart, 1990), suggesting that selection should favour individuals able to perform effective grooming. However, grooming posture impairs visual scanning (Cords, 1995; Maestripieri, 1993; Mooring & Hart, 1995). Few studies have investigated the way in

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which animals circumvent the conflict between those two fitness-related behaviours and most of them used a time budget approach (e.g. Baker & Smith, 1997). While these studies provide important insights into the 'ecology of grooming', the relative investment in antipredator or antiparasite behaviours remains largely unexplored at a finer temporal scale (but see studies on birds preening, although this behaviour encompasses functions other than anti-parasitic, e.g. references in Roberts, 2003; Randler, 2005; Dominguez & Vidal, 2007). This contrasts with the numerous studies examining the historical trade-off between vigilance and foraging at the scale of the foraging bout (Beauchamp, 2015). This study aimed at identifying the determinants of the decision to engage or not in grooming for an individual experiencing strong predation pressure. We studied individually recognizable free-ranging impalas, *Aepyceros melampus*, a heavily predated species (Fritz & Bourgarel, 2013) facing a significant threat from tick infestations, especially during the birth season (Horak, Gallivan, Braack, Boomker, & De Vos, 2003). Impala self-grooming (Mooring & Hart, 1997a), allogrooming (Hart & Hart, 1992) and maternal allogrooming (Mooring & Rubin, 1991) patterns as well as factors shaping vigilance behaviour while feeding (e.g. Pays et al., 2012) are already well studied, offering a good theoretical and practical background. We considered maternal allogrooming of offspring, because we expected the selection pressures involved in the vigilance–grooming conflict to be acute in the context of maternal care, as suggested below. We focused on maternal allogrooming occurring during suckling bouts as they constitute most of the occasions for females to groom their young once the neonate stage ends (Mooring & Rubin, 1991; Mooring & Hart, 1997b; P. Blanchard, O. Pays & H. Fritz, personal observations). In addition, this very standardized behaviour provides the opportunity to compare females in similar body postures. Further, focusing on immobile focal animals allows a more accurate investigation of the relationship between risk perception and the local environmental variables than in foraging individuals, which are typically moving.

Antagonist Selection Pressures at Play

Parental care refers to any form of behaviour by a parent that increases offspring growth or survival (Clutton-Brock, 1991). Both maternal allogrooming and maternal vigilance are expected to closely match this definition. As maternal allogrooming is further expected to increase current offspring fitness at the cost to the mother's ability to invest in future offspring (as having her head down increases her own probability of being preyed upon, e.g. Mooring & Hart, 1995), allogrooming behaviour also conforms to the definition of maternal investment (Trivers, 1972).

Natural selection pressures on maternal investment in offspring grooming are expected to be strong. By removing ectoparasites before they attach and begin to feed, maternal allogrooming may prevent offspring from several associated costs (Musante, Pekins, & Scarpitti, 2007). Although calves may be allogroomed by other individuals in the population (Mooring & Hart, 1997b), maternal allogrooming has the specificity to be directed to any part of the calf's body while allogrooming is always directed to the head and neck regions (Mooring & Hart, 1997b), i.e. unreachable by self-grooming (Hart & Hart, 1992). Moreover, both forms of allogrooming may be complementary as allogrooming involves a form of dental comb (Mckenzie, 1990) while maternal allogrooming typically involves a licking with the tongue (Mooring & Hart, 1997b), also clearly effective at removing ectoparasites (Mooring & Samuel, 1998; Rich, 1973). Maternal allogrooming serves other important hygienic functions. For instance, the concomitant removal of mud or faeces is expected to decrease the risk of diseases (Fraser & Broom, 1990) and the role of maternal saliva involved in licking in removing potentially pathogenic bacteria from the calf's coat and/or discouraging their growth has been shown experimentally (Kohari, Sato, & Nakai, 2009). Moreover, allogrooming quality is thought to be one of the maternal traits affecting offspring survival in ungulates for reasons other than hygiene (Alexander, 1988), especially for neonates (Dwyer & Lawrence, 1998, 2005). They include heat loss reduction, stimulation of activity, removing of the olfactory cues for predators, contribution to early bonding through olfactory memory (Nowak, Porter, Levy, Orgeur, & Schaal, 2000) and stimulation of urination and defecation (Metz & Metz, 1986). Interestingly, manual grooming of hand-reared impala calves increased motivation to bottle-nurse (Mooring & Rubin, 1991; see also Lent, 1974). Finally, benefits associated with allogrooming but not specific to maternal allogrooming such as a reduction in heart rate (Feh & de Mazières, 1993) may have special value in a context of the mother–young bond. Altogether, these results suggest that strong selection pressures should favour females investing in the allogrooming of their young and thus displaying a head-down posture during suckling bouts, i.e. when opportunity for maternal grooming is expected to peak (Mooring & Hart, 1997b; Mooring & Rubin, 1991).

Concomitantly, natural selection pressures on maternal care decisions to improve offspring safety are also expected to be strong. In line with the importance of (1) early offspring survival for a female's lifetime reproductive success (Clutton-Brock, 1988), (2) predation as a driver of preweaning mortality in ungulate populations (Linnell, Aanes, & Andersen, 1995) and (3) maternal vigilance for offspring survival in a predation context (Fitzgibbon, 1990), increased vigilance behaviour for lactating females compared to other females is a common feature in ungulate studies (Quenette, 1990), including impalas (Burger & Gochfeld, 1994; Hunter & Skinner, 1998). The higher predation on juveniles is probably the result of poorer skills in both escaping and identifying a predatory stimulus as a threat (Dimond & Lazarus, 1974). During a suckling bout, the escape capacity of the young (and probably of the mother) is expected to be even lower given its posture and its impaired visual field so that the young is expected to rely probably entirely on its mother's vigilance (e.g. Komárková & Bartošová, 2013). Furthermore, the vigilance costs associated with adult–adult allogrooming has been firmly established in impala (Mooring & Hart, 1995): when a person approached a group of impalas, mimicking a stalking predator, the allogroomer became alert about 8 s later than the non-allogrooming individual nearest to the allogrooming pair. Because maternal allogrooming occurs head down in impalas, scanning capacities are probably even more impaired than for adults engaged in head-up allogrooming. Altogether, these results suggest that natural selection should favour females caring for their offspring by scanning regularly, particularly during exposed behaviours, i.e. by frequently displaying a head-up posture during suckling bouts.

Drivers of Individual Decision

We considered both intrinsic and extrinsic explanatory variables, including those known to shape vigilance in foragers. These variables are presented in Table 1 together with the associated prediction. We paid special attention to the proxy of the risk perception experienced by the focal individual. Classically, intrinsic and extrinsic factors are implicitly expected to shape the risk perception of the animal and, in turn, risk perception is expected to impact the decision to engage or not in scanning: in short, when a forager often raises its head, it is inferred that it faces high risk perception when its head is down. In a maternal allogrooming–vigilance context, the amount of time the female spends

Table 1
Description of the explanatory variables considered in the analyses on allogrooming probability, together with related prediction and references

Sources of variation in maternal behaviour	Variable description	Variable name/type	Expected effect on allogrooming probability	Related sources
Extrinsic variables				
Number of adults Number of calves	First axis of a PCA explained by the number of adults and the number of calves in the group. For 9 observations, we could not accurately assess the number of individuals in the group because of visual barriers so we discarded them from analyses involving group size	'Group size', continuous	Allogrooming expected to increase with group size through detection/dilution/confusion effects. May interact with vegetation characteristics	Beauchamp (2009), Krause and Ruxton (2002) Rieucau et al. (2012)
Spatial position in the group Distance to nearest neighbour	Second axis of a PCA explained by the spatial position in the group and the distance to the nearest neighbour (always an impala adult female here). 'Central' individuals were those with an angle of maximum 90° without conspecifics and 'peripheral' individuals were those with an angle of minimum 180° without conspecifics. 31 of 101 individuals could not be assigned to either of these two classes	'Isolation', continuous	Allogrooming expected to decrease with isolation as an individual at the periphery of the group or far from its conspecifics is more exposed to a predator	Inglis and Lazarus (1981) Pöysä (1994)
Number of other ungulates	Number of other ungulates in the group (typically groups of 5–15 zebras, *Equus quagga*, and up to 10 kudus, *Tragelaphus strepsiceros* with a resident group of 10 wildebeest, *Connochaetes taurinus*, on rare occasions)	'Number of other ungulates', continuous	Allogrooming expected to increase with the number of other ungulates in the group as they are expected to be involved in detection/dilution/confusion effects	Scheel (1993)
Largescale cover	Percentage of pixels unrelated to sky on a hemispherical picture taken at the exact suckle place. Relates to the largescale habitat type: open habitats (grasslands) get low values, closed habitats (bushlands) get high values	'Largescale cover', continuous	Prediction too hazardous in this system given the large range of tactics used by impalas' predators and the ambivalent functions of vegetation	Pays et al. (2012), Krause and Ruxton (2002), Lazarus and Symonds (1992)
Medium scale cover	The closest vegetation item is recorded every 20° around the focal individual and classified as high (>1 m) or low (>40 cm and <1 m) (see text). The proportion of high vegetation items over these 18 measurements is then calculated. Relates to the characteristics of the vegetation surrounding the focal animal	'Medium scale cover', continuous	The visibility cost associated with allogrooming as compared to head-up posture is expected to increase when the proportion of high vegetation items decreases, leading to decreased allogrooming, all other things being equal. Yet, because individual/group conspicuousness is also expected to depend on this measure and on group size, a more complex pattern is expected, as for alertness level	
Fine scale cover	Distance to the nearest vegetation item obstructing the vision of the impala only if engaged in allogrooming (i.e. 'low item' >40 cm and <1 m), on the side of the sucking calf. Relates to the scale of the animal's head	'Fine scale cover', continuous	Allogrooming is expected to decrease with increasing distance to the nearest visual obstruction (and thus when its obstructive effect is strengthened). Not expected to be related to alertness level	
Intrinsic variables				
Alertness level	Alertness level is based on body postures and behaviour. Two classes when based on always observable traits (neck, ears), three when chewing behaviour could be assessed (see text)	'Alertness', factor (2 or 3 levels).	Allogrooming is expected to decrease when mothers are more alert given the increased exposure to predation when allogrooming.	Alados (1985), Blanchard and Fritz, (2007), Mooring and Hart (1995)

(*continued on next page*)

Table 1 (*continued*)

Sources of variation in maternal behaviour	Variable description	Variable name/type	Expected effect on allogrooming probability	Related sources
Calf sex	Known if the calf was captured (N=21, leading to 75 observations)	'Sex', two levels	Contradictory results in the literature, no particular prediction for impalas	Cassinello (1996), Poindron, Terrazas, de la Luz Navarro Montes de Oca, Serafin, and Hernández (2007)
Female–calf pair identity	Pairs are identified either by the ear tag (N=27) or by distinctive natural marks (N=7) on the calf and/or the female's body	'Identity', factor (34 levels)	Included in the analysis for nonindependence issue and to investigate whether the female's identity (e.g. her experience, personality, rank) and/or her calf's (beside its sex, controlled for) explained some of her behaviour	Dwyer (2008), Thouless (1990)
Suckling duration	Total duration of the suckle (s)	'Suckle duration', continuous	Allogrooming expected to increase with suckling duration. Suckling duration expected to decrease with alertness level	Lent (1974)
Additional variables				
Departure behaviour	Whether mother (typically followed by the young) fled at the end of the suckling	'Departure behaviour', two levels	Probability of fleeing expected to increase with alertness level	
Distance to observer's car	Distance from focal animal to observer's car (m)	'Distance to car', continuous	Allogrooming expected to increase with distance to car	
Date of observation	Julian date of observation	'Date', factor (22 levels)	Included in the analysis for nonindependence issue	
Place of suckling	Place where suckling occurred	'Place', factor (79 levels)	Included in the analysis for nonindependence issue	

We expected these variables to have the same effect on allogrooming duration and the reverse effect on alertness level, except when specified (namely, beside 'alertness level', for fine scale cover, suckling duration and departure behaviour).

head up during suckling bouts (i.e. without allogrooming) allows a more direct assessment of its 'alertness level', i.e. a proxy of its overall risk perception, based on its body postures and behaviour (see Methods; Alados, 1985; Blanchard & Fritz, 2007). Hence, we first investigated the role of intrinsic and extrinsic variables in shaping alertness level and then focused on the role of alertness in shaping the maternal decision to engage or not in allogrooming. Furthermore, we concur with Arenz (2003) and others that studying trade-offs between vigilance and activities other than foraging is advantageous for characterizing individual predation risk perception and its potential associated costs. Because vigilance patterns of foraging prey are shaped by predation risk perception but also by food-related parameters (e.g. Beauchamp, 2009), a change in vigilance behaviour is not a reliable currency to assess a change in risk perception. For instance, foragers are expected to increase their proportion of feeding time spent scanning in patches where food intake rate is limited by chewing and swallowing rates rather than by food encounter rate, i.e. where they benefit from 'spare time' allowing cost-free vigilance (Blanchard & Fritz, 2007; Fortin, Boyce, Merrill, & Fryxell, 2004). We thus expect alertness level assessed during suckling to be a better proxy of predation risk perception than individual investment in vigilance for foragers. Although suckling could occur during resting, rumination and foraging bouts, we did not expect food characteristics (e.g. Fortin et al., 2004) or scramble competition for food (e.g. Clark & Mangel, 1986) to interfere in the maternal decision to allogroom. The monitoring of group mates to glean information on food patches may also lead to head-up postures of foragers (Beauchamp, 2003). Although we cannot rule out such pressure during suckling, it seems unlikely in our population (Pays et al., 2012).

METHODS

Study Site and Animals

The observations were conducted in December 2007 and January 2008 in the main Camp area of the Hwange National Park (HNP), located on the northwest border of Zimbabwe (19°00′S, 26°30′E). HNP covers an area of ca. 15 000 km^2 with vegetation typical of southern African dystrophic wooded savannahs with scattered patches of grasslands. In our study site, impalas are preyed upon by a large variety of predators, including spotted hyaenas, *Crocuta crocuta*, hunting dogs, *Lycaon pictus*, leopards, *Panthera pardus*, cheetahs, *Acinonyx jubatus*, and lions, *Panthera leo* (Fritz & Bourgarel, 2013). Calves were captured at night when they stayed concealed in vegetation far from the adults, i.e. before the age of 1 week (Fritz & Bourgarel, 2013), from 15 to 28 December 2007. They were weighed, measured and ear-tagged.

Ethical Note

Approval for the study was obtained from the Zimbabwe Parks and Management Wildlife Authority (Permit 23(1) (C) (II) 12/2007 and Permit 23(1) (c) ii 31/2007). We parked the vehicle at least 100 m away to minimize disturbance (range of observation distance of 10–210 m as impalas sometimes walked towards the vehicle) and waited for the group to leave the area before recording the vegetation measurements.

Behavioural Observations

We looked for a group of females with young. When a mother was observed suckling a calf (defined as a contact between a calf's muzzle and a female's udder), we recorded the variables presented in Table 1. We only focused on suckling involving individually recognizable mother–young pairs. We never saw several instances of suckling beginning simultaneously. The observation started at the beginning of the suckling period and ended with it (duration: mean = 63.17 s, median = 62.0 s, SD = 14.8 s). Maternal allogrooming was defined as the licking (or rarely grooming involving dental comb) of any part of the calf's body (typically: the hind leg, perineal region, head, flanks and back). We did not consider the brief (about 1 s) naso-anal contact between the female and her young that occurred at the very beginning of most of the suckling

bouts. A single observer recorded 101 observations in total, involving 34 different pairs.

The overall state of alertness of the mother during suckling was inferred from body postures and behaviour assessed during the 'head-up part' of the suckling, i.e. when the mother was not allogrooming (e.g. Alados, 1985; Blanchard & Fritz, 2007). We defined as 'weakly alert' females with nonerected ears and neck (i.e. a 'v' could be drawn following the neck line from the shoulders to the head), as 'alert' females with erected neck, erected ears typically pointed forwards, head in an immobile posture or jerky changes of direction and displaying chewing behaviour (first ingestion or rumination), and finally as 'highly alert' females displaying the same attitude as 'alert' females but without chewing although we were confident that they had food in their mouth, i.e. when grass was seen coming out of the mouth or when the female resumed chewing at the end of the suckle without regurgitation of a bolus during suckling for ruminating females (Blanchard & Fritz, 2007, 2008). On 24 occasions, the female met the 'alert' criteria but either it proved impossible to confidently assess whether she could have chewed or not, or we knew that she could not have chewed (typically, she was resting without ruminating when the suckling occurred or she swallowed at the very beginning of the suckling bout). As these individuals could have been 'alert' or 'highly alert', they were not included in the analyses involving the three levels of alertness. They were, however, included when we grouped 'alert' or 'highly alert' in one category to contrast with 'weakly alert', which happened for some analyses. Observations were cancelled for six females that regularly changed postures and thus could not reliably be assigned to one of the three categories. Finally, we excluded two observations as the alert female was responding to an identified external stimulus, namely a male roaring while chasing another female.

Once the group had left the area, the same observer made the vegetation measurements at the suckling location (see below and Table 1).

Vegetation Measurements

First, we took a numerical hemispherical picture using a 'fisheye' lens positioned at 1 m high and directed towards the ground, using a spirit level to ensure horizontality. The body of the photographer, an irrelevant part of the photograph, was always positioned where the back of the mother was. We then used Photoshop software to count the percentage of pixels unrelated to the sky (i.e. related to vegetation) that were on the picture (Jennings, Brown, & Sheil, 1999). This first measurement of the vegetation gave a largescale proxy of the 'habitat type', with low values indexing grassland and high values indexing bushland.

Second, we focused on the obstructive/protective characteristics of the vegetation immediately surrounding the focal pair. Every 20° (from 0° to 360°, i.e. 18 measurements, see e.g. Blanchard, Lauzeral, Chamaillé-Jammes, Yoccoz, & Pontier, 2016 for a similar '360° approach'), we identified the nearest vegetation item above 40 cm (maximum considered distance of 100 m; average distance of 21.8 m) and calculated the proportion of 'High' cover items, classified using the criteria explained below. When the nearest 'cover' was the observer's car (25 of 1422 occasions) or was further than 100 m (45 of 1422 occasions), the proportion was calculated without this measurement (for example, 17 measurements considered instead of 18 if one of the nearest 'vegetation' items was the car).

'Low' cover items were above 40 cm and below 1 m high. These thresholds were chosen given the height of an adult impala and the height of a calf assessed in the field, so that this first category of items is expected to obstruct the view of the mother only when she is engaged in grooming. Hence, while the influence of these low vegetation items on the mother's decision to allogroom is expected to be high, its impact on prey conspicuousness and on prey/predator moving abilities are expected to be small.

'High' cover items were above 1 m high. Whatever the mother's head position (i.e. allogrooming or not), this second category of vegetation items thus obstructed the vision of both the prey and the predator. The difference in visual detection capabilities for the prey between head-down and head-up postures is thus expected to be lower than for low vegetation items. These high cover items may further represent physical barriers for both the prey and the predator.

For high values of the proportion of high cover around the focal pair, both the probability of being detected by a predator and the cost associated with a further decrease in visibility when allogrooming are expected to be low. This proxy of medium scale cover and the previous proxy of largescale cover were not correlated ($P > 0.96$).

Finally, we recorded the distance of the closest low cover item on the side of the suckling: this item should obstruct the visual field only when allogrooming, and do so more at short distances. This third measurement gave us a proxy of the vegetation structure at a fine scale, i.e. the scale of the animal's head.

Data Analyses

Given the number of explanatory variables relative to the number of observations and the collinearity issues, we first ran a standardized principal component analysis (PCA) on the number of adults, the number of calves, the distance to the nearest neighbour and the within-group spatial position to obtain synthetic variables. The first axis was negatively correlated with the number of adults and the number of calves and accounted for 49.2% of the total variability. This axis is labelled 'group size' hereafter (see Table 1). We multiplied the scores by −1 so that high values indicate large group sizes. The second axis was positively correlated with the distance to the nearest neighbour and the within-group spatial position (0 = centre, 1 = periphery) and accounted for 35.0% of the total variability. This axis is labelled 'isolation' hereafter (see Table 1). High values indicate individuals far from their closest neighbour/at the periphery of the group.

For all the dependent variables, the general procedure was the following. We tested the biologically relevant two-way interactions in succession and the main effects against the most general model by using maximum likelihood ratio chi-square tests with backward stepwise selection procedures. A variable was considered significant when $P < 0.05$. We always kept the main effects in the model when included in a significant interaction. As observations performed the same day, at the same location or on the same individuals were not independent, we included these three variables as random terms. As group size and largescale cover were correlated (larger groups being overrepresented in more open areas), we reran the model selection procedures using a subsample of our observations discarding very open areas, so that both variables were no longer significantly correlated. This did not affect our results. Including other ungulate species in the calculation of group size did not affect our conclusions either.

We expected that both intrinsic and extrinsic variables could impact the mother's alertness level, and consequently her probability of engaging in allogrooming. Hence, to avoid collinearity issues when investigating the sources of variation in allogrooming odds (with all explanatory variables including also alertness level), we first investigated the sources of variation in alertness level. In this first analysis, we compared 'weakly alert' individuals with both 'alert' and 'highly alert' individuals. We used a logistic model with

alertness level as the binary dependent variable and the following explanatory variables (see Table 1): largescale cover, medium scale cover, group size (first PCA axis), isolation (second PCA axis), distance to the car, calf sex and the interaction between group size and both cover's proxies. We did not include small scale cover here as we did not expect it to impact on alertness level.

To investigate whether alertness was an accurate proxy of the risk perception experienced by the mother, we tested whether the level of alertness impacted suckling duration (normally distributed, Shapiro–Wilk $W = 0.9781$, $P = 0.092$) and the mother's odds of fleeing, typically followed by the calf, at the end of the suckling. We hypothesized that stressed mothers should suckle for a shorter time and be more inclined to leave the patch hastily. We did not include these variables in the previous general analysis as we expected alertness to shape them, i.e. we expected them to be dependent variables instead of being explanatory variables of alertness level.

In a second step, we investigated the sources of variation in allogrooming odds. We followed the same procedure as described above and performed two analyses with allogrooming behaviour as the binary dependent variable ('0' when no allogrooming occurred and '1' when at least one allogrooming occurred). First, we considered the same explanatory variables (fixed and random terms) together with fine scale cover and suckling duration, two variables that were not expected to shape alertness level but may impact the probability of allogrooming, the former because of its effect on visibility while head down, the second because the longer the suckling bout the more likely the decision to allogroom. Second, we focused on alertness level (using first the two then the three categories) as a driver of allogrooming probability, with the same three random terms.

Finally, we focused on females engaging in allogrooming. We investigated the sources of variation in the proportion of suckling time spent allogrooming (log transformed to fit normality). Given the reduction in sample size and the results obtained in the previous analyses, we reduced the number of explanatory variables and focused on: large, medium and fine scale cover, group size, isolation and the interaction between medium scale cover and group size with the date as a random term. Alertness level was not included as too few 'alert' or 'highly alert' mothers engaged in grooming (see Results).

We used the 'glmer' function in the 'lme4' package in R software (R Core Team, 2013) for mixed models with a binary response variable (link: logit) and 'lmer' for a normally distributed response variable. Model coefficients are presented ± SE.

RESULTS

Maternal allogrooming occurred in 57 of 101 observations. Females were classified as 'weakly alert' on 43 occasions, 'alert' on 17 and 'highly alert' also on 17. The remaining 24 females were classified as 'alert or highly alert' given the lack of information relative to their chewing behaviour.

Sources of Variation in Alertness Level

There was a significant interaction between medium scale cover and group size in the final model (Table 2; intercept = 15.79 ± 6.69; coefficients: medium scale cover*group size: 5.18 ± 2.57; medium scale cover: −1.25 ± 3.20; group size: −3.13 ± 1.41), indicating that the odds of being 'alert' or 'highly alert' decreased with increasing group size when surrounded by low vegetation items and increased with increasing group size when surrounded by high vegetation items (Fig. 1). Largescale cover and calf sex were also retained in the final model (Table 2), indicating that the odds of being 'alert' or 'highly alert' decreased with increasing largescale cover (i.e. from open to closed habitats; coefficient: −0.15 ± 0.07) and for females suckling male calves (coefficient for male calves: −2.65 ± 1.11).

Table 2
Variables influencing mother's 'alertness level'

Explanatory variables	Deviance	*df*	*P* (chi-square)
Largescale cover*group size	0.82	1	0.36
Distance to car	0.02	1	0.88
Isolation	0.63	1	0.43
Medium scale cover*group size	5.02	1	**0.03**
Sex	7.27	1	**0.01**
Largescale cover	5.29	1	**0.02**
Pair identity	*0.00*	*1*	*1*
Place	*0.00*	*1*	*1*
Date	*0.03*	*1*	*0.87*

Random terms are in italics. Fixed effects retained in the final model and associated *P* values are in bold.

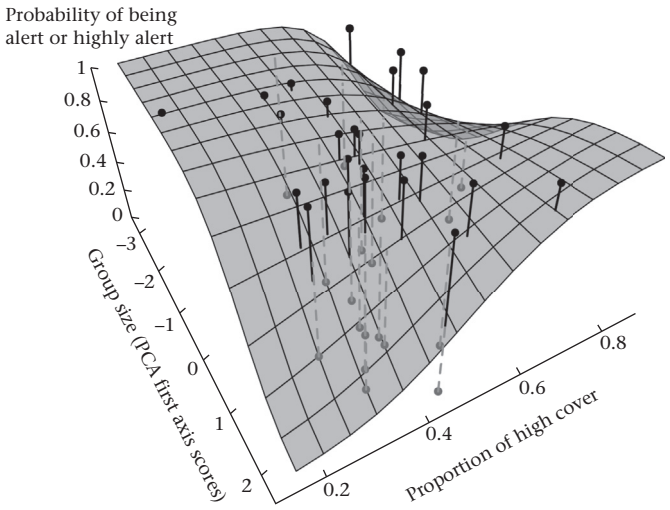

Figure 1. Probability of a suckling female being 'alert' or 'highly alert' according to group size (PCA first axis with high values referring to large group sizes) and to the proportion of surrounding cover consisting of high items. Black points refer to 'alert' or 'highly alert' females and grey points to 'weakly alert' females. The chequered surface represents the predictions according to the final model selected as shown in Table 2, thereby including largescale cover (set at average value) and calf sex (set at average predicted values of both sexes).

The isolation, the distance to the car and the interaction between largescale cover and group size were not retained in the final model (all $P > 0.36$; Table 2). The three random terms (pair identity, place and date) were not significant (all $P > 0.87$; Table 2).

Alertness Level as a Proxy of Risk Perception

'Alert' or 'highly alert' mothers suckled their calf for a shorter time (deviance = 5.96, $df = 1$, $P = 0.015$; intercept = 67.83 ± 2.33, coefficient for 'alert' or 'highly alert' mothers = −7.74 ± 2.86) and tended to leave the patch hastily (no test performed as no 'weakly alert' mother left the patch while the eight females that left the patch in 101 observations were all 'alert' or 'highly alert'). When we ran our models for females with information about chewing behaviour, thereby distinguishing between 'weakly alert', 'alert' and 'highly alert' mothers, alertness level was marginally significant, indicating a decrease in the suckle duration with the mother's alertness level (deviance = 5.18, $df = 2$, $P = 0.075$; intercept = 67.75 ± 2.40, coefficient for 'alert' mothers = −3.23 ± 4.10, coefficient for 'highly alert' mothers = −10.05 ± 4.10).

Sources of Variation in Allogrooming Probability

In the first analysis considering all the biologically relevant interactions and variables except alertness level for collinearity reasons, suckle duration was the only explanatory variable retained in the final model, with allogrooming odds increasing with the total amount of time spent suckling (intercept $=-3.96 \pm 1.59$, coefficient for suckle duration $= 0.07 \pm 0.03$). The interactions between largescale cover and group size and between medium scale cover and group size were not significant (both $P > 0.58$; Table 3). The odds of allogrooming were not related to isolation, distance to the car, large, medium or fine scale cover, group size or calf's sex (all $P > 0.13$; Table 3).

In the second analysis, we focused on the effect of alertness level on the odds of allogrooming. We first considered 'weakly alert' versus 'alert' together with 'highly alert' mothers. There was a clear negative effect of being 'alert' or 'highly alert' on the odds of allogrooming (deviance $= 46.44$, $df = 1$, $P < 0.0001$; intercept $= 2.69 \pm 0.63$, coefficient for 'alert' or 'highly alert' mothers $=-3.62 \pm 0.69$). When we distinguished between the three levels of our proxy, there was a clear negative effect of alertness level on the odds of engaging in allogrooming (deviance $= 55.67$, $df = 2$, $P < 0.0001$; Fig. 2).

Table 3
Variables influencing mother's allogrooming decision

Explanatory variables	Deviance	*df*	*P* (chi-square)
Largescale cover*group size	0.003	1	0.96
Medium scale cover*group size	0.30	1	0.58
Isolation	0.13	1	0.72
Distance to car	0.23	1	0.63
Largescale cover	0.33	1	0.57
Group size	0.21	1	0.64
Medium scale cover	0.71	1	0.40
Fine scale cover	2.27	1	0.13
Sex	2.31	1	0.13
Suckle duration	8.07	1	**0.005**
Pair identity	*0.01*	*1*	*0.93*
Place	*0.00*	*1*	*1*
Date	*0.00*	*1*	*1*

Random terms are in italics. The fixed effect retained in the final model and the associated *P* value are in bold.

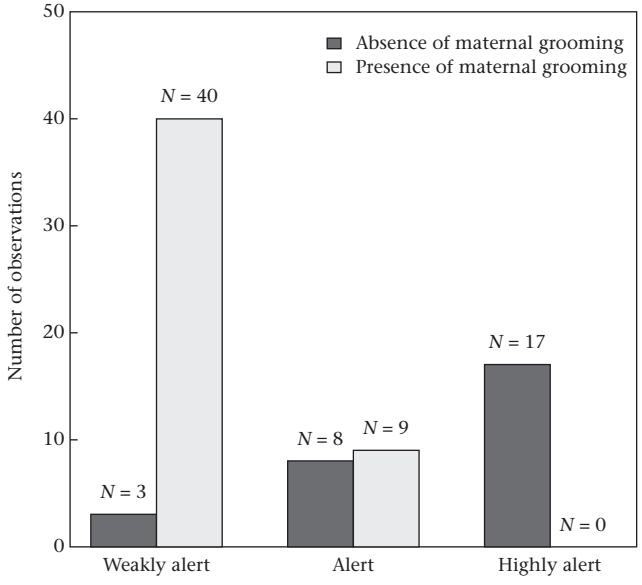

Figure 2. Number of observations with maternal allogrooming (grey bars) and without maternal allogrooming (black bars) according to the mother's alertness level. Sample sizes are given above each bar. Observations for which the female could not be confidently classified as 'alert' or 'highly alert', given the lack of accurate information about chewing investment, were not included in this analysis ($N = 24$).

Table 4
Variables influencing the proportion of suckling time spent allogrooming for mothers engaged in grooming

Explanatory variables	Deviance	*df*	*P* (chi-square)
Fine scale cover	0.12	1	0.73
Isolation	2.53	1	0.11
Largescale cover	2.66	1	0.10
Medium scale cover*group size	4.59	1	**0.03**
Pair identity	*0.00*	*1*	*1*

Random term is in italics. The fixed effect retained in the final model and the associated *P* value are in bold.

Females Engaging in Allogrooming

There was a significant interaction between medium scale cover and group size in the final model (intercept $= 1.88 \pm 0.43$; coefficients: medium scale cover*group size: -1.17 ± 0.53; medium scale cover: 0.02 ± 0.90; group size: 0.50 ± 0.24), indicating that the proportion of suckling time spent allogrooming increased with increasing group size when surrounded by low vegetation items and decreased with increasing group size when surrounded by high vegetation items. Fine and largescale cover and isolation did not affect the proportion of time spent allogrooming for those mothers engaging in allogrooming (all $P > 0.10$; see Table 4).

DISCUSSION

Few studies have investigated the factors triggering the individual decision over the vigilance–grooming conflict at a fine scale (references in Dominguez & Vidal, 2007; Randler, 2005; Roberts, 2003). Yet (1) ectoparasites are known to shape the fitness of hosts, (2) grooming has been shown to be highly effective at removing ectoparasites and (3) the trade-off between vigilance and grooming has been firmly established. Moreover, besides documenting the overlooked 'ecology of grooming', focusing on this system allows a better investigation of the factors shaping risk perception in prey than the classic vigilance–foraging trade-off for which food-related parameters are decisive. Overall, our data suggest a stronger role of habitat characteristics and group size than individual intrinsic characteristics in shaping predation risk perception in female impalas and their concomitant adjustment in parental care.

Largescale Cover and Visual Contact in Foragers

In line with the ambivalent functions of cover (Lazarus & Symonds, 1992), studies on vigilance displayed by foraging impalas in relation to largescale cover have had very different results (Pays et al., 2012; Shorrocks & Cokayne, 2005). Still, a lower vigilance in more open habitats is often reported (Underwood, 1982), including in HNP (Périquet et al., 2012). Our data revealed that females suckling their calf in closed largescale habitats, i.e. bushland, were less alert than in open grassland habitats. If we assume that the scanning rate of foraging individuals and alertness level during suckling are both a measure of individual predation risk perception, this discrepancy between our results and those previously published for HNP may be explained by the focus and timing of our study, i.e. mothers during the rearing period. Because calves' escape skills might be limited when facing a coursing predator (Fitzgibbon, 1990; P. Blanchard, O. Pays & H. Fritz, personal observations), open

areas were probably at high risk for them. Conversely, their smaller body size might make them more difficult to detect in the bush for a predator. Together with their random displacements, especially during frequent playing bouts, this may lead to decreased chances of being targeted and stalked, and thus to a lower exposure to predation risk (as compared to open areas and perhaps to more visible and predictable adults) and, consequently, to decreased anxiety for their mother. Périquet et al. (2012) conducted their observation later in the season, when surviving calves were more independent. In this context, both adults and juveniles might be more at risk when exposed to an ambushed predator in bushland (i.e. high values of our 'largescale cover' proxy) than to a chasing predator in grassland (i.e. low values). Interestingly, Matson, Goldizen, and Putland (2005) observed impalas during the rearing period as in the present study and reported higher vigilance further from cover.

Here we argue that the scanning rate of foraging individuals and the alertness level assessed during suckling are qualitatively different measures of individual predation risk perception. While we expect alertness level to closely match risk perception by suckling females, vigilance while foraging may be shaped by additional factors (Beauchamp, 2009). We suggest that the easier visual contact between group members in open areas plays a central role for foragers both through a more accurate perception of total group size (e.g. Elgar, Burren, & Posen, 1984) and through a social facilitation process (Clayton, 1978; Pays, Beauchamp, Carter, & Goldizen, 2013). Without visual barriers, foragers may have a precise perception of group size and consequently of the associated costs (i.e. scramble competition for food, Clark & Mangel, 1986; for impalas, see Blanchard, Sabatier, & Fritz, 2008; Smith & Cain, 2009) and benefits (Table 1), both shaped by the number of group mates (together with interindividual distances, e.g. Fernández-Juricic, Beauchamp, & Bastain, 2007). Besides facilitating the assessment of actual group size, open habitats may also lead to actual higher benefits for a given group size (see next section). Hence, we expect pressures triggering head-down postures to be stronger in open habitats, in order for the foragers 'to obtain their share of the available forage' (Clark & Mangel, 1986, p. 63) and pressures for head-up postures to be lower as 'the herd substitutes for cover, providing concealment for the individual' (Estes, 1974, p. 166) together with additional protection (Table 1). Further, a 'social buffering effect' (e.g. Kikusui, Winslow, & Mori, 2006), again through visual contact (da Costa, Leigh, Man, & Kendrick, 2004), may also lead to a faster recovery after a stimulus that triggered vigilance. This overall increased amount of time spent head down in open habitats should be further amplified by an imitation process among foraging group members (e.g. Gautrais, Michelena, Sibbald, Bon, & Deneubourg, 2007), which is again expected more when visual contact is allowed (Fichtel, Zucchini, & Hilgartner, 2011; Michelena, Noël, Gautrais, Gerard, Deneubourg, & Bon, 2006). The above reasoning holds for constant food density and group distribution/density, yet we have no data about these parameters in relation to habitat type in our system.

We report no 'isolation' effect on mothers' alertness level or grooming decision/duration, thus questioning the functional link between vigilance and risk perception in the geometry of the foraging herd. Although individuals at the edge of a group are classically expected to be more exposed to predators (Krause & Ruxton, 2002), competition may also explain lower vigilance in the centre of foraging groups (see Blanchard et al., 2008 in the same population), as commonly reported in this species (e.g. Matson et al., 2005) and others (e.g. Underwood, 1982). The greater vulnerability of mothers suckling calves might also override the protection effect afforded by a more central position, or more generally by close neighbours, when group mates are not burdened with offspring.

Medium Scale Cover, Group Size and Risk Perception

Females were less alert and more inclined to spend a greater proportion of the suckling time allogrooming their calf with increasing group size when surrounded by low vegetation items (i.e. cover impairing their visual fields only when grooming their calves but allowing easy overall detection of/by predators) while group size had the reverse effect in high vegetation items (i.e. situations impairing the mother's and predator's visual field whatever the maternal behaviour). Individual safety is classically expected to increase with group size as an approaching predator has more chance of being detected, a given group member has less chance of being targeted by the predator and the predator has more chance of getting confused when the attack leads to a sudden explosive flight (Krause & Ruxton, 2002). Numerous studies on various taxa have confirmed these expectations, with lower individual investment in vigilance with increasing group size (Beauchamp, 2015), including in impalas (e.g. Pays et al., 2012; Matson et al., 2005; but see Smith & Cain, 2009). Therefore, if alertness level and the subsequent investment in allogrooming are mostly shaped by predation risk perception, as we hypothesize, female impalas are expected to be less alert and allogroom more in larger groups. The results for pairs surrounded by low vegetation confirmed these expectations, underlining the importance of predation-related pressures in explaining the group size effect (Beauchamp, 2003; Roberts, 2003). Namely, given the high predation risk faced by the calf if the group is chased by a coursing predator (Fitzgibbon, 1990), a female should only decrease alertness and engage in allogrooming (which means, in this situation, stopping efficient scanning above the vegetation) when benefiting from valuable protection, i.e. when in large enough groups. The opposite results for female–calf pairs in high vegetation may appear surprising at first. However, the classic benefits associated with group foraging (detection, dilution, confusion) are gained only once the group has been detected by a predator. Few empirical studies have considered the extent to which group size may shape the probability of being detected/attacked by a predator: studies investigating detection ability in a predator–prey context are biased towards prey species. Although larger groups at constant population size mean fewer groups and thus a decreased prey–predator encounter probability (e.g. Ioannou, Bartumeus, Krause, & Ruxton, 2011), some studies have suggested higher risk for larger groups. Creel and Creel (2002) reported that wild dogs detected large impala groups earlier than smaller groups and, once detected, attacked them more often. Creel and Winnie (2005) suggested that elk, *Cervus elaphus*, in the Gallatin Canyon, Montana, U.S.A. dissociated into smaller groups to reduce the likelihood of being detected by wolves, *Canis lupus*. When surrounded by low vegetation items, i.e. below its height, the 'conspicuousness cost' of grouping should be minor as an impala is anyway easily detectable by a predator, even when isolated or in small groups. At the same time, classic benefits associated with grouping (Krause & Ruxton, 2002) should increase with group size, particularly in such habitats (Elgar et al., 1984; Estes, 1974; Lima, 1995). Hence, predation risk perception (here defined as the ratio between the costs and benefits of grouping associated with a predation threat) should decrease with group size, allowing individuals to progressively engage in important activities conflicting with safety at the scale of the body posture. When prey are surrounded by high vegetation items, the pressures they experience should differ. Because more abundant high vegetation surrounding a given focal individual means increased probability of being

hidden, more group mates in its vicinity may increase its own probability of being detected, and thus its alertness. This is because a larger group means (1) increased smell/noise/movements, all cues that a predator may exploit, and (2) increased chance for a predator of having a prey in its line of sight (because more prey occupy a larger part of its visual field, e.g. Ioannou & Krause, 2008, which is not specific to high vegetation, but specifically here because group members occupy different angles relative to high vegetation items). Hence, over a given group size range, we expect the probability of a predator detecting a group member to increase more steeply with group size in high than in low vegetation. Once the first group member is spotted by the predator, the probability of the others being detected increases (i.e. unsuccessful 'visual' hunt hypothesis sensu Valeix et al., 2011 or area-concentrated 'visual' searching sensu Benhamou, 1992). In other words, when surrounded by high vegetation, the obstructive components of cover may switch from benefiting the prey to benefiting the predator with increasing group size. From the benefits side of increasing group size, classic benefits may exist when prey are surrounded by high vegetation, but we expect them to be lowered because (1) dilution/confusion components may be minor under the threat of an ambushed predator as compared to situations where prey escape from a coursing predator and (2) the 'collective detection' assumption of the detection effect (i.e. all group members are alerted when a member detects a threat, e.g. Lima, 1995) should be relaxed because of visual barriers. Therefore, the costs of grouping might exceed the benefits in such situations, except for very small groups.

More generally, although nonadaptive reasons for group size changes in relation to habitat characteristics may exist (Gerard, Bideau, Maublanc, Loisel, & Marchal, 2002), the above speculations (together with pressures specific to foraging, see e.g. Isvaran, 2007) could also explain larger group size in open than closed habitats as commonly reported in foraging ungulates, and first noticed by Estes (1974) and Jarman (1974).

Calf Sex, Maternal Alertness and Sex Allocation Theory

Allogrooming probability/duration and overall alertness level may be shaped by many intrinsic characteristics of the ungulate mother, including parity (Dwyer and Lawrence, 2000), hormone levels (Dwyer, 2008), temperament (Murphy et al., 1994), parasite load or age (Festa-Bianchet, 1988). Although we did not measure these parameters, the absence of a pair identity effect on maternal alertness level or behaviour (controlling calf sex) may suggest an overall greater role of environmental (or temporal) variables than of intrinsic pair characteristics in shaping risk perception and the subsequent decision to allogroom. Nevertheless, mother impalas suckling female calves were more alert during suckling. As offspring sex does not seem to be a determinant of maternal vigilance in a foraging context (e.g. Hamel & Côté, 2008), we had no predictions for the effect of sex. Our data did not allow us to investigate differences in calf behaviour and/or morphology associated with sex that could lead to a difference in vulnerability to predation and/or to harassment by conspecifics, and thus in the need for vigilance by the mother. Alternatively, some characteristics of the mother could be related to both the probability of producing a calf of a particular sex and her overall anxiety level. To our knowledge, relative reproductive costs of producing males and females or the respective fitness return of each sex in relation to characteristics of the mother have not been studied for this species. However, the sexual dimorphism present in all age groups together with the competition among males for access to females (Fritz & Bourgarel, 2013) suggest that pressures relating to the reproductive costs hypothesis (Myers, 1978) or Trivers and Willard model (Trivers & Willard, 1973) may occur. Hence, good-quality females could benefit from producing male offspring, with the reverse being expected for poor-quality females. Concomitantly, several parameters indexing maternal quality in a sex allocation context may also impact anxiety. For instance, primiparous and thus potentially young females with limited investment capabilities may be more anxious given the novelty of the situation (e.g. Dwyer and Lawrence, 2000; Mooring & Rubin, 1991), the higher predation risk faced by their young (Warren, Mysterud, & Lynnebakken, 2001) or possibly their lack of skills in suckling behaviour such as milk release (Cameron, 1998). Social rank may lead to similar results as it may also correlate with both anxiety and offspring sex (e.g. in red deer, Thouless, 1990; Kruuk, Clutton-Brock, Albon, Pemberton, & Guinness, 1999). We hope that specific individual data will allow researchers to validate or invalidate these suggestions in the future.

The Way Forward

Some studies have underlined the existence of non-nutritive suckling, whose functions might be physiological or social (Cameron, 1998). The suckling events we recorded may thus belong to two distinct categories, long nutritive suckles, mostly initiated by the mother following the physiological need to empty the mammary gland and allowing her to select less risky habitats or times (see also Hejcmanová et al., 2011), and short non-nutritive 'alarm suckles' initiated by the calf in response to a fearful stimulus, resulting in higher anxiety for the mother as she does not choose the place (and thus the predation risk level) or the time (and thus the predation risk level again but also possibly her ability to release milk). Furthermore, the mother may be inclined to gather information about the stimulus driving the alarmed state of her calf (Adler, Linn, & Moore, 1958; Shackleton & Haywood, 1985; see also Lent, 1974 in impalas). Future studies should pay attention to individual movements and postures of both the calf and the mother just before suckling occurs in order to identify the initiator (Lent, 1974; Réale & Boussès, 1995). Furthermore, recording movements of the pair after a mother refuses to suckle, together with the characteristics of both habitats and maternal alertness level, may also be helpful.

Impalas are more intensively infested by ticks than other medium-sized antelopes (e.g. Horak et al., 2003), ticks may strongly affect host fitness (e.g. Hart, 1990) and grooming is clearly effective at removing ticks (e.g. Mooring et al., 1996). Yet, the question of the fitness consequences of behavioural adjustments of mothers to predation risk in terms of reduced calf allogrooming during suckling remains. We may hypothesize that reduced allogrooming during a suckling bout due to high risk perception may be compensated for by higher allogrooming investment later. However, we did not observe maternal allogrooming outside suckling bouts (see also e.g. Mooring & Rubin, 1991), in line with the weak mother–young association reported in this species (Mooring & Rubin, 1991), and probably no more than three to four suckling events per day occur at this stage (Mooring & Rubin, 1991; P. Blanchard, O. Pays & H. Fritz, personal observations). Moreover, if grooming mostly aims at removing ticks before they attach and engorge, frequent grooming bouts are probably more efficient than few more thorough ones (see above). Finally, although calves may be groomed by other individuals in the population (Mooring & Hart, 1997b), maternal allogrooming has important specificities (see above). Hence, in years with high levels of tick infestation, high predation risk around the rearing period may probably significantly impact maternal fitness through calf parasitism costs. However, designing a protocol addressing these questions accurately would probably face ethical challenges.

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